

SHORT COMMUNICATION

Getting to the root of tree neighbourhoods: hectare-scale root zones of a neotropical fig

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Sessile organisms interact locally on the scale of their body sizes, and one of the great advances in population and community ecology is the use of individual-based models to examine species interactions (Biondini 2001, Bolker & Pacala 1999, Pacala & Deutschman 1995, Pacala & Silander 1985, 1987; Silander & Pacala 1985). Canopies are often taken as a proxy for body size in the plant literature, even though roots can make up substantial amounts of a plant's biomass, have productivity that equals or exceeds the above-ground parts, and are critical in both competition and mutualisms involving nutrient capture and water balance (Biondini 2001, Casper & Jackson 1997, Casper *et al.* 2003, Rajaniemi & Reynolds 2004, Robinson 2004). Root zones, however, are seldom incorporated in plant ecological studies because they are exceptionally difficult to measure, and the importance of intra- and interspecific root interactions is little known (Schenk & Jackson 2002).

Here we report the results of a field study on the spatial extent of roots in the neotropical fig, *Ficus schultesii* Durand (Moraceae), a canopy emergent common at the landscape-level in western Amazonia. We find that the area of their rooting zone exceeds their canopy area by a factor of 14–64-fold. While *Ficus schultesii* may be an extreme case, this example shows that representing plant size with canopy size can grossly underestimate the scale of plant interactions in tropical forests. The expansive root-zones of canopy emergent trees may make them keystone taxa in the structure of tropical soil microbial communities.

The study was conducted in mature floodplain forest at the Cocha Cashu Biological Station in Manu National Park, Peru. While lying within the meander-belt of the

Manu River, the forest has flooded only three times for 1–3 d during the last 30 y. The study site has a mean annual temperature of 23.4 °C and receives ~2300 mm y⁻¹ precipitation, mainly during a pronounced 8-mo wet season (Terborgh 1990, Terborgh *et al.* 1996). Sampled trees were all on substrate with minimum ages of >400 y (and likely much older) based on topographic position and radiocarbon dates from a nearby oxbow lake.

Ficus schultesii is a broadly buttressed canopy emergent fig with large (25–35 mm diameter), bat-dispersed fruits (synconia) that house an obligately mutualistic wasp pollinator. Stem diameters in adults exceed 1 m above the buttresses, which often extend upwards to 8 m above the ground. *Ficus schultesii* is found in both terra firme and floodplain forests, with a landscape density of 1 tree per 7.5 ha (Pitman *et al.* 1999, 2001). This is above the median density of all 1021 tree species recorded in the area, though it never exceeds more than 1 individual ha⁻¹ in the 43 forest inventory plots available for the area (Pitman *et al.* 1999). The roots of *F. schultesii* start at the base of the buttresses and extend across the soil surface for long distances over the forest floor, branching infrequently. The combination of a uniquely warty reddish root bark, bright white latex, and the low local density of conspecifics permits roots to be followed easily across the forest floor, even when running short distances below ground.

We chose the four individuals of *F. schultesii* near the station trail system to measure root length and root zone. As the trails were cut on a grid for bird and primate censuses, they are unlikely to be biased towards the large trees. *Ficus schultesii* has myriad superficial roots extending away from its bole. We chose the four largest roots at each tree, recorded their orientation, and measured along the length of each root, taking a straight-line distance any place the root disappeared underground.

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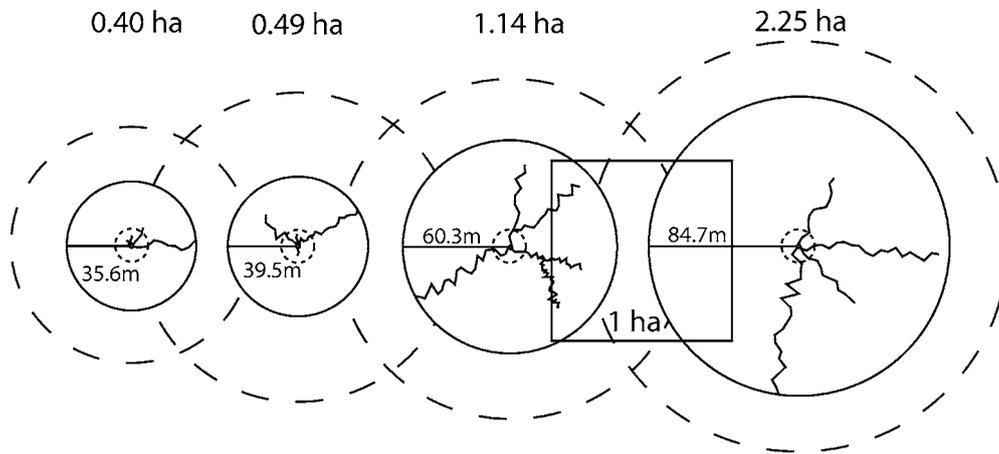


Figure 1. Root lengths and rooting zones for four *Ficus schultesii* trees. Rooting zone (ha) described by radius of longest root is shown above each tree. Inner dashed circles are crown diameters, outer dashed circle is estimated rooting zone from allometric equation accounting for roots disappearing below soil (0.8 ha, 1.8 ha, 2.2 ha, 2.8 ha, respectively).

We measured root diameter every 5 m along its length and where the root entered or left the soil. Straight-line distance (radius) from the last known position of the root to the parent tree was also measured. Potential rooting zone was taken as the area of a circle calculated from the straight-line distance from the bole to the longest root where it disappeared below ground.

The median root length was 54.3 m with a range of 7 m to 102.3 m, with the median straight-line distance at disappearance of a root being 50 m (range = 35.6–84.7 m; Figure 1). This gave a median root zone area of 0.8 ha per tree (range = 0.4–2.3 ha). Crown radii for the trees were estimated from an inverse prediction equation based on stem diameter to crown diameter relationships for 433 trees from a 2.25-ha tree plot central to the *F. schultesii* used in the study (J. Terborgh, *pers. comm.*). The estimated crown radii (95% C.I. = 10–12 m) corresponded closely to the measured radius for one of the trees in the study (10 m).

Direct measurements of root length and their derived measures are conservative as roots disappeared below ground before their terminus; at 50 m roots averaged 8.3 ± 1.0 cm diameter. Additionally, there was a negative correlation between the length of a root and its diameter at disappearance ($r = -0.62$, $P < 0.01$), suggesting that short roots in particular continued considerable distances underground. To estimate the continuing underground length of the roots, we fitted a linear equation to root length-diameter relationship for each root and estimated the total length of the root. The estimated median root length increased to 73.5 m (range = 17–132 m). To estimate the radius of the root zone we applied the average root length to straight-line distance from the measured roots to the estimated root length. This gave a median radius of 79.7 m (range = 50–95.7 m), and a median root zone area of 2.0 ha (range = 0.8–2.8 ha).

The use of canopy size to define plant neighbourhoods greatly underestimates the potential interactions of *Ficus schultesii* in tropical forests. Measured roots zones in this study exceeded the crown zones by 3–8-fold in linear distance and 10–60-fold in area. Accounting for lengths of roots continuing underground increased the estimates to 4–9-fold and 20–75-fold, respectively. Indeed, the measured root zone of an average individual of *F. schultesii* is approximately the same as the area of the standard hectare forest inventory plot used for trees ≥ 10 cm diameter in the tropics, and the estimated root zone is double the size of a standard forest inventory plot. The roots extend so far through the forest that the trunk is not visible from their ends. The measured length of *F. schultesii* roots exceed any reported in the literature (Casper *et al.* 2003, Schenk & Jackson 2002, Stone & Kalisz 1991).

Grossly underestimating the extent of plant interactions can have important consequences for understanding maintenance of diversity and community structure in tropical forests. Predictions of leading theories of community and population structure are based on the extent of spatial interactions among species (Barot 2004, Hubbell 2001, Leigh *et al.* 2004). Based on crown area, a typical *F. schultesii* would interact with 20–25 of the approximately 600 individuals found in a typical hectare of western Amazonian forest; based on the measured root zone, this number climbs to ~ 500 individuals. Even making the most conservative assumptions: modelling only the four *F. schultesii* roots measured in this study as lines, and taking rooting zones of all other species to be equal to the median crown diameter in floodplain forest (6 m), the four *F. schultesii* roots intersect the root zones of 65 other trees. If the methods and estimates used in this study overestimate the root zone by a factor of two, the conclusions remain the same: root-zone influence of

F. schultesii can be dramatically larger than that of the crown.

Why roots of *F. schultesii* traverse such a large area is unknown. Structural support for the large above-ground portion of the tree is a possible factor, but 100 m of root would appear to greatly exceed the point of diminishing returns for investment versus tensile support. Trees may also be searching for specific nutrient microsites in the soil. We suggest water relations as the most plausible of the hypotheses based on the demands placed on the fig due to its reproductive biology. *Ficus schultesii* produces abundant crops of large, bat-dispersed fruits from synconia pollinated by an obligate wasp mutualist that lives within the synconium (Herre 1996). Large fruits with low surface to volume ratios have been experimentally shown to rely on transpirational cooling through stomata on the fruit surface (Patino *et al.* 1994). Disruption of transpiration, as would occur under severe water stress, kills the obligate mutualist, eliminating pollen flow and, in extreme cases, causing loss of the fruit crop.

The consequences of large root zones to tree communities depend critically on the importance of root-mediated interactions to population and community structure. In temperate systems roots have been shown to mediate both direct and indirect competition and mutualisms among plants with important consequences for community structure. Direct interactions include competition for water and nutrients (Biondini 2001, Caldwell *et al.* 1996, Casper *et al.* 2003, Mahall & Callaway 1992, Pregitzer *et al.* 2002). Equally important may be the indirect interactions, both positive and negative, mediated through root interactions with soil microbial communities through both root exudates and the sheer input of biomass through root turnover (Fisher & Fule 2004, Garbeva *et al.* 2004, Griffiths *et al.* 1999, Herre *et al.* 2005, Kiers *et al.* 2000, Mangan *et al.* 2004, Partel & Wilson 2002, Piotrowski *et al.* 2004, Robinson 2004, Ruess *et al.* 2003). Tropical tree roots are likely to alter soil microbial communities in the same species-specific ways that their temperate counterparts do (Booth 2004, Herre *et al.* 2005, Lovelock *et al.* 2003). Below-ground productivity of tropical trees through root-turnover can equal or exceed leaf productivity, moving tonnes of carbon into the soil (Clark *et al.* 2001, Matamala *et al.* 2003, Matthews 1997, Silver *et al.* 2005, Vitousek & Sanford 1986). Roots of single *F. schultesii* trees may affect soil microbial communities throughout entire hectares of tropical forest, potentially influencing interactions of hundreds of individuals and species of trees. If the function of *F. schultesii* roots is more directed towards specialized foraging, *F. schultesii* may have strong pairwise interactions with trees that can not even be seen from its bole.

At least 82 species of trees in 26 families found in the ~1000 ha surrounding Cocha Cashu reach above-

ground sizes similar to *F. schultesii* (>70 cm dbh; Pitman & Silman, unpubl. data). Casual observation of superficial roots indicates that rooting zones exceeding crown area may be common in the genus *Ficus*, the most diverse large tree genus in western Amazonia. Whether the root system of *F. schultesii* is anomalous in extent awaits further study. The sheer size of the rooting zones of canopy emergent trees in general – even if not as dramatic as that of *F. schultesii* – may make them keystone species for soil microbial community structure. Indirect effects resulting from plant-microbe interactions may represent an important neighbourhood effect acting on scales significantly larger than individual tree canopies.

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